Brain

A Journal of Neurology

EDITED BY

GORDON HOLMES, M.D.

WITH THE HELP OF

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All Editorial Communications, Manuscripts and Printed Matter to be addressed to the **Editor, GORDON HOLMES, M.D., 9, Wimpole Street, W. 1.**

Subscriptions, &c., to be sent to Messrs. MACMILLAN & CO., Ltd., St. Martin's Street, W.C.

MACMILLAN AND CO., LIMITED
ST. MARTIN'S STREET, LONDON
NEW YORK: THE MACMILLAN COMPANY

1927

Price per Part, 6s. net.
Yearly Subscription, 24s. net.

Vol. L. Part 1.

THE RELATIONSHIP BETWEEN THE STRENGTH OF THE CONDITIONED STIMULUS AND THE SIZE OF THE RESULTING CONDITIONED REFLEX.[1]

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From any indifferent stimulus it is possible to form a conditioned salivary reflex ("food reaction") in the dog. Such a stimulus must be above the threshold of excitation for the brain, and it must not give rise to any innate (unconditioned) reaction of greater potency than the unconditioned food reflex, e.g., a pain or a sexual reflex.[2]

When the conditioned reflex has been established, saliva begins to flow after a latent period of from two to ten seconds following the application of the stimulus. The measurement of the salivary flow is made as follows: A small glass balloon is fastened with wax to the salivary fistula. It has two outflow tubes, one of which is connected to a manometer outside the dog's cabinet, while the other and lower tube remains closed except when opened to allow of the syphoning off of the collected saliva.

The flow of saliva into the balloon increases the pressure in the system and causes a movement of the fluid in the horizontal manometer, one graduation of which corresponds to 0·01 c.c. of saliva. The quantity of saliva secreted is the measure of the potency of the conditioned stimulus.

Strong and Weak Stimuli.

In the early investigations upon conditioned reflexes it was found that in a dog showing a salivary reaction to several conditioned stimuli one of the latter was more potent than the others. For example,

[1] Read before the Scientific Assembly of the Institute of Experimental Medicine, Leningrad, May, 1926.

[2] To supplant psychological by physiological terminology, it is the custom in Pavlov's laboratory to speak of a reflex to pain as a "reflex to destructive stimuli."

auditory stimuli: a metronome, an electric bell, or various musical tones, elicit a more speedy and abundant salivary response than do optical or cutaneous stimuli, such as flash-lights, images, scratching, &c. Least potent are thermal stimuli. On this basis laboratory stimuli were divided into strong (auditory) and weak (optical and cutaneous).

~~These differences were originally regarded as the expression of different intensities of stimulus.~~ One may assume that in the case of sound stimuli there is a greater amount of external energy transported to the peripheral receptors than in the case of cutaneous or thermal stimuli, and that as a result a nervous impulse of greater intensity is sent into the central nervous system in the former case. That the conditioned reaction depends upon the strength of the acting stimulus receives direct confirmation in the laboratory. Thus, it has been shown (Tichimirov and Zelony [6], [8], [9]), that in the response to a certain tone there is a greater reflex effect when the strength of the tone is increased, the pitch remaining constant, and a correspondingly smaller effect when the tone is weakened. This is true for other stimuli in the same analyser. Kasherinova [2] proved this for tactile and Orbeli [3] for optical stimuli. Zelony found that if a conditioned reflex be formed on a chord of several tones, a single tone of the chord elicits a weaker response than the whole cord. In the case of a chord composed of two tones of unequal strength, of the two tones tried separately the stronger is the more potent as a stimulus. Thus there are a number of observations which indicate that the size of the conditioned reflex depends upon the physical strength of the stimulus. There are, however, other observations which suggest a relationship between stimulus and response of greater complexity than that outlined above. In the first place the application of weak stimuli, more particularly tactile and thermal, evokes a state of drowsiness in the animal. It is now possible to assert that the process of "internal inhibition" is the basis of the process of sleep, and, proceeding from this, we may suppose that the nervous elements of the skin and the thermal receptors of the cerebral cortex possess special functional properties. They cannot remain long in a state of excitation and pass quickly over into one of inhibition. Upon what factors this depends is too complex a question for discussion here.

On what does the difference in the size of the reflex reaction to stimuli belonging to different analysers depend? This difference was formerly explained as an expression of individual functional properties of the nervous elements of the different analysers in the cerebral cortex. It might be supposed, for example, that the nervous elements of the

tactile and thermal analysers cannot produce so strong a process of excitation as those of the auditory analysers, and that they more readily pass over into a state of inhibition. Such a view lacks experimental verification.

Certain observations suggest that the difference depends solely upon the strength of the stimulus, upon the amount of energy sent into the cortex. To investigate this problem we employed complex stimuli affecting several analysers. It was already known that in the reaction to a complex of two simultaneous stimuli the chief effect was produced by one of the components, that of the other being suppressed, so that the latter did not produce the reaction which it would have done had it been employed alone. If we assume that the magnitude and stability of the conditioned reflexes to auditory stimuli when compared with the responses to cutaneous and optical stimuli depend, not upon a qualitative difference in the nervous processes concerned, but upon quantitative-factors, then we may experimentally vary the latter, comparing, for example, the effect of weak auditory and strong optical stimuli. If quantitative factors govern the response, then we should obtain a greater response to strong light than to weak auditory stimuli. Further, if our supposition is true, these two stimuli might be so adjusted as to produce equal reflex responses.

The observations recorded in the present paper were based upon such an hypothesis.

Observations had already been made in the laboratory relating to this problem, but being directed to other purposes, did not provide the facts which were of primary interest to us. Thus, Palladin [4] formed a conditioned reflex by the summation of stimuli (simultaneous thermal —cold—with scratching stimuli). When each component was separately employed it was found that a response equal to that obtained on combination of the two resulted from scratching, while cold alone gave either no response or a minimal one. However, the continued use of cold as a stimulus finally evoked a constant response, but one less than that elicited by scratching. Thus in a complex of qualitatively different stimuli the response depends upon the more potent stimulus. Perlzweig [5] confirmed these observations. We have extended them to include auditory and optical, auditory and thermal combinations. In one dog we formed a conditioned reflex to a faint sound (Galton's whistle) applied simultaneously with a strong light (400 candle-power), the sound of the whistle being muffled by placing it in a large bottle so that it was scarcely audible to the human ear at 40 cm. distance from

the bottle. Observations In ~~another~~ the "Rogdie" dog a reflex-s ~~was~~ ere established to an electric bell and a metronome 160, and a negative conditioned reflex to the metronome 90, and then a reflex to the tone "Do" of a pitch-pipe. All these reflexes were built upon the unconditioned food reflex (feeding with a moist meat-bread powder).

First ~~*Observation* 1.—Using the dog "Rogdie,"~~ the following complex conditioned stimulus was employed: thirty flashes per second of a 400 candle-power lamp with a tone of Galton's whistle (1,500 vibrations). A reflex was established after the second trial and rapidly became stable, that is, it gave constant manometer readings. After the thirteenth combination of this stimulus with feeding, the light stimulus alone unaccompanied by feeding was tried. It gave the same response as the complex light-sound stimulus. On the following day, the complex stimulus having retained its potency, the tone stimulus alone was employed. It gave a secretion of six divisions on the manometer, that is, a response 12·5 per cent. of the response to the light-sound complex.

These observations are recorded in the following table :—

TABLE I.—DOG "ROGDIE."

Time	Number of trials	Conditioned stimulus	Duration of stimulus	Latency of response	Manometer reading	With feeding = + Without ,, = −
(Oct. 22, 1925)						
4.33	35th	Bell	30 sec.	16 sec.	28	+
4.40	43rd	Metronome 160	30 ,,	5 ,,	58	+
4.50	13th	Light and tone	30 ,,	4 ,,	47	+
5.02	44th	Metronome 160	30 ,,	4 ,,	48	+
5.10	1st	Light alone ..	30 ,,	3 ,,	48	−
5.13	36th	Bell	30 ,,	2 ,,	87	+
5.17	45th	Metronome 160	30 ,,	5 ,,	54	+
(Oct. 23, 1925)						
3.40	46th	Metronome 160	30 ,,	2 ,,	22	+
3.46	14th	Light and tone	30 ,,	4 ,,	48	+
3.56	47th	Metronome 160	30 ,,	5 ,,	58	+
4.04	1st	Tone alone ..	30 ,,	13 ,,	6	−
4.07	37th	Bell	30 ,,	1 ,,	67	+
4.15	20th	Metronome 90	30 ,,	28 ,,	1	−
4.19	48th	Metronome 160	30 ,,	10 ,,	28	+
4.25	49th	Metronome 160	30 ,,	7 ,,	50	+

The strength of the tone was then slightly increased and the new complex stimulus tried fifteen times, and then the tone alone unnacompanied by feeding. The complex gave a manometer reading of 50, the tone alone one of 8 (16 per cent.).

The tone was again increased so that it became clearly audible

outside the dog's cell through the open door in the next room. The strengthened complex was repeated eighteen times, and then the two components tried separately, this time accompanied by feeding.

TABLE II.—DOG "ROGDIE."

Time	Number of trials	Conditioned stimulus	Duration of stimulus	Latency of response	Manometer reading	With feeding = + Without ,, = –
(Nov. 5, 1925)						
4.02	61st	Metronome 160	30 sec.	5 sec.	77	+
4.10	30th	Light and tone	30 ,,	6 ,,	50	+
4.23	62nd	Metronome 160	30 ,,	7 ,,	47	+
4.30	2nd	Tone alone ..	30 ,,	8 ,,	8	–
4.35	24th	Metronome 90	30 ,,	8 ,,	2	–
4.36	44th	Bell	30 ,,	2 ,,	86	+

TABLE III.

Time	Number of trials	Conditioned stimulus	Duration of stimulus	Latency of response	Manometer reading	With feeding = + Without ,, = –
(Nov. 20, 1925)						
9.20	80th	Metronome 160	30 sec.	3 sec.	52	+
9.25	61st	Bell	30 ,,	2 ,,	83	+
9.33	49th	Light and tone	30 ,,	3 ,,	54	+
9.41	62nd	Bell	30 ,,	2 ,,	80	+
9.47	1st	Tone alone ..	30 ,,	3 ,,	12	–
9.57	37th	Metronome 90	30 ,,	3 ,,	18	–
10.02	81st	Metronome 160	30 ,,	2 ,,	75	+

TABLE IV.

Time	Number of trials	Conditioned stimulus	Duration of stimulus	Latency of response	Manometer reading	With feeding = + Without ,, = –
(Nov. 23, 1925)						
10.00	63rd	Bell	30 sec.	4 sec.	56	+
10.06	82nd	Metronome 160	30 ,,	2 ,,	62	+
10.14	2nd	Tone alone ..	30 ,,	7 ,,	13	+
10.19	64th	Bell	30 ,,	5 ,,	55	+
10.26	3rd	Light alone ..	30 ,,	4 ,,	35	+
10.30	38th	Metronome 90	30 ,,	—	—	–
10.38	3rd	Tone alone ..	30 ,,	6 ,,	20	+
10.43	83rd	Metronome 160	30 ,,	2 ,,	60	+
10.48	4th	Tone alone ..	30 ,,	3 ,,	20	+
(Nov. 28, 1925)						
10.10	87th	Metronome 160	30 ,,	3 ,,	60	+
10.18	69th	Bell	30 ,,	4 ,,	62	+
10.24	9th	Tone alone ..	30 ,,	5 ,,	26	+
10.30	7th	Light alone ..	30 ,,	5 ,,	42	+
10.40	42nd	Metronome 90	30 ,,	—	—	–
10.48	70th	Bell	30 ,,	6 ,,	42	+
(Dec. 8, 1925)						
10.15	96th	Metronome 160	30 ,,	3 ,,	58	+
10.20	11th	Light alone ..	30 ,,	3 ,,	62	+
10.28	77th	Bell	30 ,,	4 ,,	78	+
10.35	16th	Tone	30 ,,	3 ,,	60	+
10.42	48th	Metronome 90	30 ,,	4 ,,	14	–
10.52	97th	Metronome 160	30 ,,	3 ,,	70	+
11.00	78th	Bell	30 ,,	3 ,,	80	+
11.07	13th	Light alone ..	30 ,,	2 ,,	53	+

In Table~~s~~ III ~~and IV~~ is seen that when the light and tone stimuli are separately employed, in spite of the increase in strength of the latter, at first the predominant effect was obtained from the light, the tone producing a very small increase in response. Thus, in the first experiment the light alone gave a manometer reading of 25, that is, 71 per cent. of the response to the complex stimulus on the same day of observation. The tone gave a reading of 12, or 22 per cent., of the response to the combined stimuli.

On the basis of the foregoing experiments we may conclude that ~~both~~ light (400 candle-power lamp) ~~and cold (0° C.) are~~ is a more potent stimulus than a very faint sound~~s~~. Thus, auditory stimuli are not essentially and qualitatively prepotent. The larger reflex secretory effect obtained on such auditory stimuli as the metronome and the bell depend solely upon their relatively greater strength than light and thermal stimuli. Rikman found the same to be true of tactile stimuli.

Further, our experiments showed that the effect of a stimulus is not entirely dependent upon its quality, that is, upon whether it affects cutaneous, auditory or optical analysers. Cold, the weakest of all stimuli, was combined with a very faint sound (vibration of the metallic disc of a telephone receiver) which could be decreased to threshold value, and since thermal stimuli are prone to induce a state of drowsiness in the animal, the complex was employed for a short time only (ten to fifteen seconds). The results were comparable with those obtained by a light-tone complex.

The faint telephone vibration is a weaker stimulus than the application of cold (0° C.). In the first observations cold gave a manometer reading of 21, telephone of 7 only. After the separate application of each stimulus, the relative strength of the response to the telephone alone increased, but remained less than that to the cold stimulus.

In the experiment shown for March 15 (Table V), cold gave a reflex corresponding to 34 divisions of our scale, and the telephone a reflex corresponding to 22, and this relation between the two persisted until the end of our work.

We should like to call attention to the following fact in the mechanism of the reflex to complex stimuli. When we tried for a long time separately the light and the tone, the effect of the tone was seen gradually to increase, until finally the tone began to give almost the same effect as the light. Table IV.

TABLE V.

Time	Number of trials	Conditioned stimulus (c.s.)	Duration of action of c.s.	Latent period of conditioned salivary secretion	Manometer reading	With feeding = + Without ,, = −
(Feb. 10, 1926)						
3.44	5th	Do (pitch-pipe)	30 sec.	4 sec.	76	+
3.24	24th	Cold-telephone	15 ,,	8 ,,	12	+
3.31	6th	Do (pitch-pipe)	30 ,,	5 ,,	50	+
3.36	25th	Cold-telephone	20 ,,	6 ,,	23	+
3.42	69th	Metronome 90	30 ,,	7 ,,	8	−
3.48	55th	Bell	30 ,,	5 ,,	46	+
3.53	26th	Cold-telephone	30 ,,	7 ,,	34	+
(Feb. 18, 1926)						
4.30	35th	Cold-telephone	10 ,,	6 ,,	2	+
4.40	57th	Bell	30 ,,	4 ,,	57	+
4.47	36th	Cold-telephone	30 ,,	7 ,,	22	+
4.52	72nd	Metronome 90	30 ,,	20 ,,	3	−
5.02	120th	Metronome 160	30 ,,	8 ,,	52	+
5.07	8th	Do (pitch-pipe)	30 ,,	6 ,,	48	+
(Feb. 19, 1926)						
4.44	58th	Bell	30 ,,	5 ,,	42	+
4.48	37th	Cold-telephone	30 ,,	—	—	+
5.05	121st	Metronome 160	30 ,,	5 ,,	60	+
5.10	38th	Cold-telephone	30 ,,	8 ,,	3	+
5.18	1st	Cold (alone) ..	30 ,,	7 ,,	21	+
5.29	1st	Telephone(alone)	30 ,,	9 ,,	7	+
(Feb. 26, 1926)						
4.40	45th	Cold-telephone	15 ,,	—	—	+
4.48	125th	Metronome 160	30 ,,	10 ,,	37	+
4.53	4th	Cold (alone) ..	30 ,,	7 ,,	22	+
4.58	75th	Metronome 90	30 ,,	6 ,,	6	−
5.04	11th	Do (pitch-pipe)	30 ,,	4 ,,	40	+
5.10	46th	Cold-telephone	15 ,,	8 ,,	2	+
(Feb. 27, 1926)						
4.34	47th	Cold-telephone	15 ,,	8 ,,	6	+
4.42	12th	Do (pitch-pipe)	30 ,,	6 ,,	50	+
4.50	4th	Telephone(alone)	30 ,,	7 ,,	11	+
4.59	29th	Light (alone) ..	30 ,,	6 ,,	42	+
(Mar. 15, 1926)						
4.47	17th	Do (pitch-pipe)	30 ,,	6 ,,	54	+
4.53	134th	Metronome 160	30 ,,	3 ,,	78	+
5.00	11th	Cold (alone) ..	30 ,,	8 ,,	34	+
5.08	135th	Metronome 160	30 ,,	5 ,,	63	+
5.14	12th	Telephone(alone)	30 ,,	4 ,,	22	+

From these observations we may conclude that in the complex stimulus the weaker component cannot exert its own full effect because it is in a state of partial suppression by the stronger component. Such an inhibition of the weaker by the stronger component is in all probability a general rule when two or more stimuli are combined in a complex. There is, as a consequence, a constant struggle or conflict between different points of excitation in the cerebral cortex.

There may be not only a suppression of the weaker component, but also a mutual influence of one on the other, the weaker stimulus may

in some measure diminish the influence of the stronger. Observations made by Yakovleva [7] and by ourselves incline us to this view. We found that when the strength of a tone was greatly increased the response to a complex stimulus of which it is a component becomes for the next few days irregular and smaller. Evidently new relations are set up between the components, and a certain length of time is necessary to establish a new equilibrium between light and tone.

These experiments do not afford a conclusive answer to the question of the specificity of function of different parts of the brain, but they suggest that all parts of the cerebral cortex function in the same way and are subject to the same factors. The possibility of differences of functional activity is not excluded, but if such differences exist they are of a quantitative order only. In reality the determining factor is the energy which acts upon the nervous elements of the cortex. Further and more exact observations are necessary for a final decision of the question. For example, we must have exact quantitative estimations of the energy which acts upon the various peripheral receptors on stimulation, the extent to which this energy is transformed into the nervous impulse, and its strength when it reaches the cerebral cortex. If it could be demonstrated that there is an exact correspondence between the size of the reaction and the intensity of the nervous impulse which reaches the cortex, we might conclude that cerebral activity is conditioned entirely by external factors.

Summary.

(1) Separate employment of the components of a complex conditioned stimulus is a reliable method of determining their relative strengths.

(2) In a complex of two stimuli, the main effect is produced by the stronger stimulus, and this may even inhibit the weaker component.

(3) A strong light (400 candle-power lamp) and cold (0° C.) are more potent stimuli than a very faint sound.

(4) The size of the conditioned reflex reaction depends upon the strength of the stimulus, that is, upon the energy transmitted to the cerebral cortex.

(5) The comparative effects of different stimuli depend upon the intensities of these stimuli, regardless of the analyser to which they belong.

(6) Our observations incline us to the view that the various regions

of the cerebral cortex function, in the main, identically and such differences as may exist from region to region are of a quantitative order only.[1]

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[1] We desire to thank Dr. F. M. R. Walshe for certain suggestions as to the phraseology in this article.

Printed by JOHN BALE, SONS & DANIELSSON, LTD., 83-91, Great Titchfield Street, Oxford Street, London, W.